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BACTERIAL PHYLOGENY AS INDICATED BY MODERN TYPES[1]

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THE importance of the group we call bacteria in any theories concerning the origin and evolution of life on our planet is well shown by several recent writers on the subject, notably Jensen (1909), Osborn (1916), and Kligler (1917). In each case, however, there are certain misinterpretations of our knowledge of the modern bacteria and their function which go far to invalidate, or at least to weaken, the specific conclusions which they reach with reference to the types of primitive bacteria.

In our search for hints as to ancestral types by investigation of modern species of bacteria we must hold in mind that although present-day bacteria approach most closely to what we conceive must have been primitive life, nevertheless and for this very reason the group of modern bacteria must have the longest evolutionary history of any existing group. That any modern species closely resembles the original type is therefore not extremely probable. It can not be too often emphasized that in speculations concerning evolutionary history based upon modern forms with no adequate fossil ancestral types we must deal only with the tips of the ultimate twigs of the branches of the evolutionary tree. By a careful comparison of the surviving forms we may gain a knowledge of their probable relationships, but it should be remembered that in no case this relationship is that of parents and offspring, but that of brothers and cousins. Perhaps we may speculate upon the probable arrangement of the branches of the evolutionary tree that have disappeared in past geologic ages by study of the survivors, but it is self-evident that there should be a perfect knowledge of these survivors, morphological and physiological, so that we may not be led astray by superficial resemblances when there exist, in fact, deep-seated and fundamental distinctions.

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[1] From the Bacteriological Laboratories.

The geologic evidence that has been adduced as to the character of the primitive bacteria is of but the slightest value. Speculation as to the primitiveness of nitrogen fixers, for example, based upon the geologic evidence introduced is scarcely convincing.

It should also be noted that it is quite possible that the bacteria do not constitute an homogeneous group in the sense that all are descended from a single primitive type of bacterium. It may be that there have been included in the group bacteria forms which have assumed similar morphological or physiological characters without having a common ancestry. Botanists, for example, at the present day are by no means convinced that seed plants have all had a common origin; in other words, the ability to produce seeds may have arisen independently in two or more groups of the fern plants. It is possible that some of the forms we term bacteria have been derived from the fungi, others from the blue-green algæ or possibly some even from the protozoa. In short, it may be that the actual relationships existing between various bacteria may be very distant.

A study of these modern bacteria will reveal relationships such as those just indicated. The possibility that the bacteria are a derived group must be constantly held in mind. To prove that they are primitive it must be shown that no group from which they might have sprung or to which they seem to be related can be regarded as more primitive. This has not been satisfactorily accomplished in certain cases.

Modern systematic bacteriologists are in fair agreement that there should be recognized five or six distinct groups or orders of bacteria. Of these, the *Eubacteriales,* or true bacteria, are generally regarded as the least specialized and possibly the most primitive. It is possible that the great group of the sulphur bacteria, the order *Thiobacteriales,* is equally primitive, though the genera and species have been less studied and are not as well known. There are unquestionably many intergrading forms between the *Eubacteriales* and the *Thiobacteriales,* as shown by close parallel series of morphological types. It seems equally clear that there are intergrading forms between the *Thiobacteriales* and the blue-green algæ. Morphologically, too, one may find every gradation between the typical colorless, sulphur-containing *Beggiatoa,* through species of this genus showing bacteriopurpurin, through the faintly colored, slender *Oscillatoria* to the thick, deeply pigmented forms. If these intergradations and indicated relationships are real, it is apparent that the true bacteria may have come from the blue-green algæ through the sulphur forms, or the blue-greens may have come from the true bacteria, or the sulphur forms may be closer than either of the other groups to the primitive types from which all three groups have been derived. While there is no definite proof apparently possible at the present time, it is not at all improbable that the last assumption is the true one. A relationship quite certainly exists between the group of sheathed filamentous bacteria (the *Chlamydobacteriales*) and the blue-green algæ. The resemblance is so well marked that certain species of the iron bacteria are quite commonly included by algologists among the algæ. The relationship to the *Eubacteriales* is not quite so clear. Possibly the genus *Sphærotilus* (*Cladothrix*) may be regarded as a link, for this organism consists of rod-shaped cells occurring in chains, all embedded in a gelatinous sheath. Motile cells (gonidia) with polar flagella somewhat resembling *Pseudomonas* types may be developed.

The fungi apparently are related to certain of the bacteria through the *Actinomycetales.* This latter group has some resemblance to certain of the true bacteria such as the *Lactobacillus* of sour milk and the diphtheria types. It is possible that these organisms together with a few genera from the *Eubacteriales* represent an entirely distinct series. The *Spirochætales* apparently constitute a group showing combinations of characters which relate them to the *Eubacteriales* and the *Thiobacteriales* on the one hand, and the *Protozoa* on the other. The group *Myxobacteriales* is apparently related to the true bacteria, but not to higher groups of plants or animals, unless there may be some as yet undiscovered relationship between these forms and the slime molds as suggested by a superficial study of their fruiting forms.

The interrelationships just discussed among the various great groups of bacteria may be illustrated by the following diagram in which the connecting lines are intended to show relationship, but not necessarily derivation.

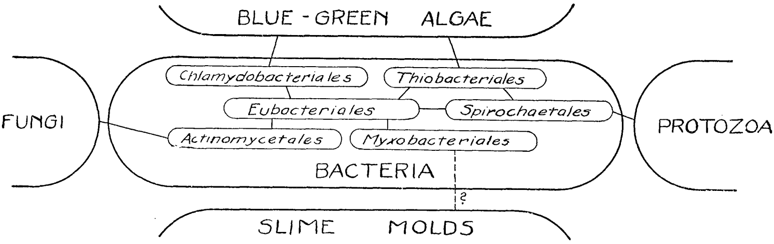

FIG. 1. CHART ILLUSTRATING THE PROBABLE INTERRELATIONSHIPS OF THE GREAT GROUPS OF BACTERIA AND THEIR RELATIONSHIPS TO OTHER GROUPS, as Fungi, Blue-green Algae and Protozoa.

From the standpoint of the student of evolution the order *Eubacteriales* (possibly also *Thiobacteriales*) is of special interest, for within it is probably to be found greater variation in physiological activity than in any other group of plants or animals. A comparison of the modern forms belonging to this group may well give some hint as to their evolution. Too much can not be expected, however, without getting far into the realms of speculation.

After rather careful consideration a committee of the Society of American Bacteriologists has proposed a list of names to be recognized as valid for the genera of this order. They have also suggested that these genera be grouped in seven families. Altogether twenty-eight genera are recognized. It should be possible, if adequate knowledge is at hand, and the *Eubacteriales* constitute an homogeneous group, so to arrange these genera as to show their probable and their possible relationships, and perhaps gain some knowledge thereby of their origin and evolution.

From the standpoint of the evolution of bacteria we are much interested in the organisms which can live and grow in the total absence of organic matter, those which utilize inorganic substances exclusively in the manufacture of their own food, in short, those bacteria which are strictly prototrophic.

Let us consider the possible sources of the various elements needed in the building up of the primitive bacterial protoplasm. We have no reason to suppose that such primitive bacterial protoplasm differed in any marked degree from the protoplasm of modern forms. Such organisms must have available carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus and iron, with small quantities of a few other elements. Upon the earth before the advent of other plant life, the carbon necessary for growth would probably be secured from carbon dioxide, or possibly from methane or carbon monoxide; the hydrogen was undoubtedly present in abundance in water, perhaps traces also of the free element, of methane, or of ammonia may have been available; the nitrogen was probably present in sufficient quantities either as ammonia or as nitrates, and of course in the form of less available, relatively inert, gaseous nitrogen; the sulfur probably existed as sulfids, sulfates, and free sulfur; the phosphorus was probably found in phosphates and the iron in both ferrous and ferric condition. It is evident that elements and compounds were present in abundance and variety, but not in the form of *organic* compounds. All modern living organisms are divided into those which require their food to be ready manufactured for their use, and those which can manufacture their own food (prototrophic). It is apparent that the primitive organism was probably prototrophic.

The manufacture of food from inorganic materials requires the expenditure of energy. We must account, if possible, for the sources of such energy for the prototrophic forms. Among modern organisms the energy needed is secured always from one of the two sources, light rays or chemical oxidation. While other types of energy are known, apparently plants have not been adapted to their utilization. If light rays were first used as an energy source, the primitive organism was probably provided with some pigment which was of significance in the absorption of the light and in its conversion into chemical energy. Among modern forms which may have resembled such primitive organism may be cited the simpler types of the blue-green algæ and the phototactic sulphur bacteria containing the pigment bacteriopurpurin. If the Chamberlin planetesimal hypothesis of earth origin is accepted, such might very possibly have been the primitive types. However, primitive conditions may have been such that light energy was not available. Organisms developing under such conditions must have been directly dependent upon chemical energy. Such energy might be secured by the oxidation of ferrous iron, of free sulphur or of the sulfids (particularly hydrogen sulfid), methane, hydrogen, carbon monoxid and ammonia. Organisms among modern species are known which can utilize each of these methods of securing energy. There is no reason, therefore, why any one of these should not be a method used by a primitive form. The modern types of organisms which oxidize ferrous to ferric iron are in many respects among the most highly differentiated of the filamentous bacteria and show many points of resemblance to the blue-green algæ. They show few primitive characters, and are probably to be regarded as not closely related to the primitive bacteria.

A study of the organisms which at the present time are known to secure energy by the oxidation of H_2S, CH_4, H_2, CO and NH_3 show that they possess certain characteristics in common. For the most part the organisms are cocci or rods, occasionally spiral, in some cases motile, and then always with polar flagella. While there are some exceptions to the rule, the organisms for the most part do not thrive in a medium containing much organic matter. It is not improbable that the primitive organism had characters not greatly unlike these enumerated. Just what type of oxidation is most primitive it is difficult if not impossible to determine, although certain conjectures may not be out of place. Probably one of the most common of the easily oxidized substances of the primitive earth was hydrogen sulfid. It undoubtedly was a common constituent of thermal springs. The modern representatives of the groups which thrive in water containing hydrogen sulfid are abundant both in numbers and in species. By means of the energy which they secure from the oxidation of H_2S and S they probably take up CO_2 and transform it into food and protoplasm. Apparently all of the forms which have been investigated are motionless cocci or rods or spirals motile by means of *polar* flagella. No modern form is known which produces spores. Many of the species contain a pigment bacteriopurpurin and swim or grow toward light, showing positive chemotaxis or chemotropism. We may find every gradation between the modern representatives of these forms and the blue-green algæ, on the one hand, and the true bacteria, on the other. Many of the blue-green algæ contain a purple coloring material in addition to the blue and green pigments. From the standpoint of evolutionary requirements, therefore, it is evident that some primitive organism having much the same type of metabolism as the modern sulphur bacteria would be a satisfactory starting form.

Before additional stress is laid upon a sulfur bacterium as a possible progenitor of modern forms, we should examine carefully other possibilities. It is conceivable (though scarcely probable) that hydrogen may have constituted a larger percentage of the atmosphere in times past than now. Several species of modern bacteria have been described which in the presence of hydrogen and oxygen may secure their growth energy by combining these elements directly or indirectly. These species are motile rods with *polar* flagella. These modern members of the genus *Hydrogenomonas,* however, are very far from primitive because under ordinary conditions they are pantotrophous growing well on ordinary laboratory media. Thus far no organism strictly prototrophic capable of utilizing hydrogen has been found. This does not prove that such organism has not existed, but throws the burden of proof upon any one who would urge hydrogen oxidation as a primitive method of securing growth energy. The results of Kaserer (1906) seem to indicate that the organism catalytically causes the transformation in the presence of hydrogen of carbonic acid into formaldehyde, the cell then using the formaldehyde as food.

Methane and carbon monoxide are also oxidized by certain of our modern bacteria, the organisms securing their growth energy in this manner. These organisms according to the descriptions are autotrophic and do not thrive in the presence of organic material. It is possible that these represent primitive characters. The organisms are rods, motile or non-motile, when motile with *polar* flagella. If either methane or carbon monoxide were common in the atmosphere of the early earth, forms of this general type may have flourished. That these gases were sufficintly abundant does not seem probable, but the possibility must be admitted.

Several types of modern bacteria are known which oxidize ammonia to nitrites and nitrites to nitrates, utilizing the energy thus secured for chemosynthesis of food from inorganic materials. At least one species of the nitrifying bacteria is a coccus, others are rods, motile by means of polar flagella. It is not at all improbable that ammonia may have been abundant enough on the primitive earth to have constituted an adequate energy source for the primitive bacteria.

Which of these modern types most closely resembles the primitive organism living on autotrophic existence? It is perhaps impossible to say. The modern representatives of the nitrifiers and the methane and carbon monoxid oxidizers are apparently rather isolated groups without numerous species and apparently not closely related to other forms. The sulfur oxidizers, on the other hand, are abundant, of many types, and show many intergradations with other bacteria and the blue-green algæ. Possibly a somewhat better case can be made out for them. However, it should be noted that all of these forms have certain characters in common, they are all autotrophic, all are aerobic, and when motile are elongate cells with polar flagella. It is perhaps a fair inference that the aerobiosis and the polar flagellation are primitive characters. We may well conclude with Jensen that all of these organisms discussed are related and may be placed in a single group. Expressed in terms of modern representatives of the primitive types, the following diagram might express the idea.

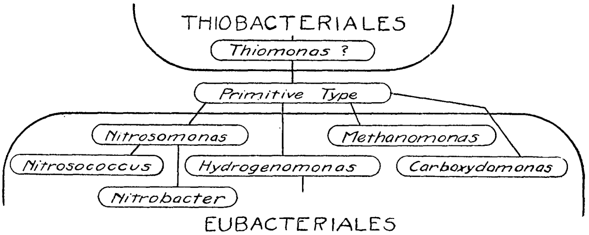

FIG. 2. PROBABLE RELATIONSHIP OF CERTAIN MODERN GENERA OF BACTERIA TO THE PRIMITIVE ORGANISM AND THEIR RELATIONSHIPS TO EACH OTHER.

We may next concern ourselves with possible and probable relationship of these various forms to other members of the *Eubacteriales,* disregarding the *Thiobacteriales.* The remainder of the *Eubacteriales* differ from the autotrophic forms thus far discussed in that in every case they require the presence of organic carbon compounds in the substrate in which they grow. These compounds may be of the greatest diversity of types, but none of the bacteria are capable of manufacturing their own carbon food. It is possible that other types of bacteria than the prototrophic may not have developed upon the earth until after the evolution of higher plants, such as the algæ, upon which they could depend for food. Possibly there may have been some start made, however, in the utilization by one type of organism of the dead bacterial protoplasm of another type.

How may we detect relationships of modern metatrophic bacteria to these more primitive types? Possibly by a study of intergrading forms. The genus *Hydrogenomonas* apparently is either autotrophic or metatrophic according to the conditions of the environment. Some primitive organism may have acquired properties similar to those of the modern *Hydrogenomonas* and constituted the progenitors of the modern forms. Possibly this type of differentiation may have arisen in several groups. It is conceivable, for example, that some organism having characters such as *Nitrosococcus* might have given rise to an independent branch, possibly to forms like *Micrococcus*. This, of course, is pure speculation.

Among the metatrophic bacteria we are probably justified in placing the genus *Pseudomonas* as most closely related to the forms discussed because of its close morphologic resemblance, with rod-shaped cell and polar flagella, to the autotrophic forms; then too, there is the evidence of the intergrading *Hydrogenomonas*. Somewhat less diversified in nitrogen metabolism are the related genera *Azotabacter* and *Rhizobium*, both usually with polar flagella, rod-shaped bodies, primitive nitrogen requirements, and marked capacity to utilize carbohydrates, oxidizing them quite completely to CO_2 and H_2O. The supply of energy is so abundant to these organisms that in the absence of sufficient combined nitrogen in the substrate they can fix atmospheric nitrogen, and build it into their protoplasm.

This nitrogen fixation must be carefully differentiated from the nitrification previously discussed. Probably the non-motile group *Mycoderma* which resembles the other organisms in ability to oxidize sugars (preferably ethyl alcohol), but is non-motile, should be placed here. These three genera are obligate aerobes and secure their growth energy by relatively complete oxidation of carbohydrates, alcohol or even acetic acid. They apparently constitute a natural group related to *Pseudomonas*. It should be recalled that a statement of relationship does not imply derivation, but simply common ancestry.

We have now considered all the bacteria which show the primitive characters of polar flagellation and obligate aerobic utilization of carbonaceous foods. In the genus *Pseudomonas* we find evidences of differentiation in metabolism, particularly ability to bring about proteolysis. In some species we have evidences of adaptation to anaerobic conditions, among the so-called denitrifiers. Some members of this group are capable of taking oxygen from nitrite and nitrates under anaerobic conditions, with evolution of free nitrogen. Other forms are known that can reduce sulfates to sulfids. Such facultative anaerobes, securing oxygen from an easily reduced compound, evidently make use of the oxygen in the same manner as though growing under aerobic conditions for the oxidation of carbon compounds. The next step in the development of anaerobiosis was probably the utilization of carbon compounds, securing growth energy by intramolecular oxidations; in such forms fermentative capacity becomes well marked.

The close relationship in morphology and physiology existing between the short spiral *Vibrio* and *Pseudomonas* indicates that the family *Spirillaceæ* has come from an ancestry having much in common with *Pseudomonas*.

The other bacteria belonging to the *Eubacteriales* are more specialized in general morphology and in physiology than the forms thus far mentioned. When motile the cells are peritrichous rather than with polar flagella.

Some forms have developed the ability to produce endospores (family *Bacillaceæ*) and seem to comprise a closely related group of genera whose relationship to the more primitive types is somewhat problematic. Another well-marked group of bacteria includes the large series of (usually) gram-negative bacteria that produce no spores. These may be included in a family *Bacteriaceæ*. With the exception of polar flagella, there is no very marked difference between the *Pseudomonas* forms and the *Proteus* types. It is quite possible that they are closely related. The cocci apparently form another homogeneous group, the *Coccaceæ*. The affinities of the group may be sought in several places. For example, there is apparently very close resemblance culturally and physiologically between the chromogenic cocci and the chromogenic rods closely related to the genus *Bacterium*; the organism usually termed *Bacillus prodigiosus* (*Serratia marcescens*) is remarkably near certain red cocci as *Rhodococcus roseus*. The possibility that there is a relationship between the *Nitrosococcus* and *Micrococcus* has already been pointed out. Then there is a decided relationship evident between the aciduric bacilli and the genus *Streptococcus*. All of these origins are possible; if all these relationships are true, the group *Coccaceæ* must be regarded as heterogeneous, that is, polyphyletic.

The group containing the tubercle bacillus (*Mycobacterium*) and diphtheria bacillus (*Corynebacterium*) shows undoubted relationships to the order *Actinomycetales*. If they have no common origin with other genera of the *Eubacteriales* they should be included in the order *Actinomycetales*. However, there is decided evidence of relationship through *Leptotrichia* and perhaps *Erysipelothrix* to the lactic acid bacteria. If this is a valid relationship it would indicate that the *Actinomycetales* are an offshoot of the *Eubacteriales*, or at least have a common ancestry.

The various relationships illustrating the probable phylogeny of the class Bacteria is illustrated in the ap-

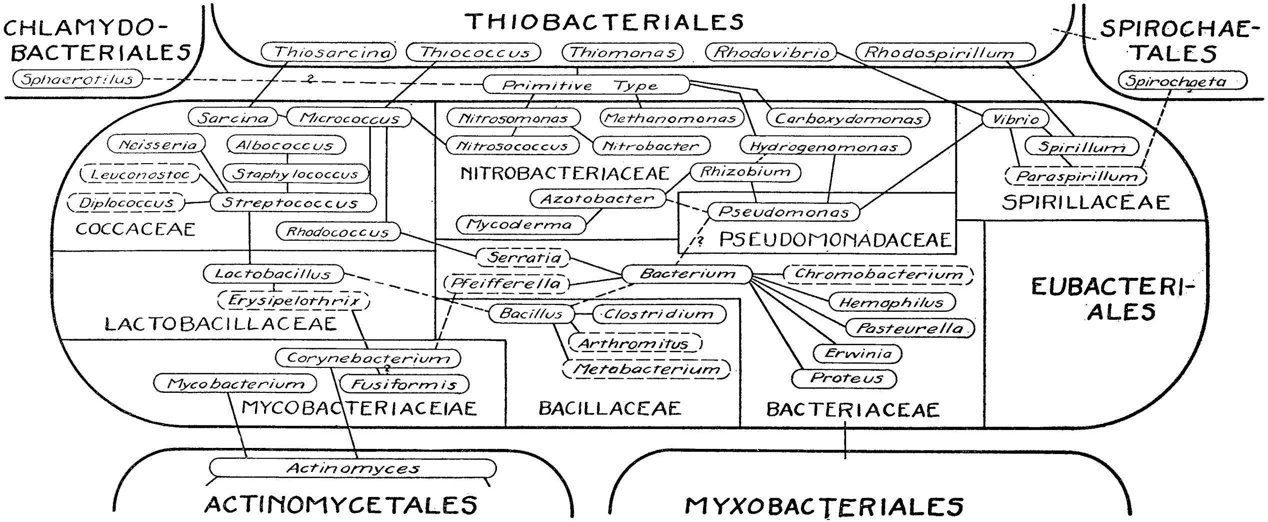

FIG. 3. SUGGESTED INTERRELATIONSHIP OF THE GENERA, FAMILIES AND ORDERS OF BACTERIA.

pended diagram. Relationships which have appeared probable to the writer have been indicated by solid lines connecting genera, possible relationships have been indicated by dotted lines. The genera comprising the families recognized by the Committee on Nomenclature as belonging to a single family are enclosed by a heavy line. Genera not recognized by the committee are enclosed in dotted lines.

The foregoing analysis would seem to indicate that the grouping of genera by the Committee on Classification, with some slight modifications possibly, represents fairly well true phylogenetic relationships of the bacteria. The exact boundaries of the families are of course of little importance providing the scheme of classification tends to show relationships.